THE ALIMENTARY CANAL OF CRIOCERUS ASPARAGI LINN.

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INTRODUCTION.

The common asparagus beetle (*Criocerus asparagi* L.) is a phytophagus insect pest of asparagus. It is widely distributed throughout the truck-growing areas of the United States.

The study that follows was made upon the suggestion of Dr. Rodney Cecil of the U. S. Bureau of Entomology, and was begun in a course in entomology at the Ohio State University, given by Dr. C. H. Kennedy on "The Morphology and Development of Insects."

The material used was collected at Geneva, New York. The beetles were opened and fixed in Kahle's solution for 24 hours, and preserved in 70% alcohol.

The author wishes to express his appreciation for the helpful suggestions and criticisms of Dr. C. H. Kennedy, under whose direction this study was made.

GROSS ANATOMY OF THE DIGESTIVE TRACT.

General Anatomy.

The alimentary canal consists of a simple tube with but few convolutions, which is characteristic of phytophagus insects. The canal is approximately one and one-fourth times the length of the insect's body. Morphologically the canal is divisible into three primary regions according to their embryonic origin. The fore-intestine (Stomodaeum) arises as an anterior ectodermal invagination; the hind-intestine (Proctodaeum) arises as a similar posterior invagination; the mid-intestine (Mesenteron or Ventriculus) which connects the two, develops as an endodermal sac from a proliferation of rings of endodermal cells, one around the posterior end of the fore-intestine and the other around the anterior end of the hind-intestine. The relation of these parts to each other is shown in Fig. 6, Plate I.

Fore-Intestine.

The fore-intestine is a short slender tube which consists of the following regions: pharynx, oesophagus, crop, and oesophageal valve.

The pharynx is the slight enlargement of the fore-intestine just posterior to the mouth which connects the mouth with the oesophagus.

The oesophagus is a very short narrow tube connecting the pharynx with the crop. It is located in the anterior part of the prothorax, and

increases slightly in size in the posterior part of the prothorax. This enlargement is the only indication of a crop being present.

The crop, as just stated, is represented by a slight enlargment of the posterior part of the oesophagus. The variation in the size of this structure is probably due to the amount of food material it contained at the time the insect was killed. This portion of the canal lies in the prothoracic segment.

The oesophageal valve is well developed and marks the division between the fore-intestine and mid-intestine by a slight constriction. This constriction is found near the junction of the prothoracic and mesothoracic segments.

No salivary glands were found.

Mid-Intestine.

The mid-intestine forms the largest part of the alimentary tract. It is marked at its anterior end by the oesophageal valve, located near the anterior part of the mesothoracic segment, and at the posterior end by the pyloric valve and Malpighian tubules located in the seventh abdominal segment. The size of the mid-intestine or stomach varies with the different specimens dissected. This is apparently due to the different amounts of food material each stomach contained. The anterior part of the mid-intestine is usually small, and the mid- and posterior parts are large in size. (Fig. 6, Plate I). Correlated with these two regions of the stomach is a slight differentiation of the epithelial lining.

Hind-Intestine.

The hind-intestine is made up of the following regions, pyloric valve, Malpighian tubules, ileum, colon, and rectum.

The pyloric valve is recognized by the constriction at the posterior end of the mid-intestine. It is located just anterior to the attachment of the Malpighian tubules to the ileum.

The Malpighian tubules are six in number and are divisible into two groups; the first group consisting of four tubules and the second of two tubules. The first group arises from a knob-like projection of the ileum just posterior to the pyloric valve, while the second arises as an evagination slightly anterior to the first group, in the region of the epithelium of the pyloric valve.

In the gross dissection the tubules are found to be entirely distinct from the walls of the canal, except near their distal ends where they penetrate the peritoneal layer of the colon. The approximate course of the tubules to the point where they enter the peritoneal layer, is shown very diagrammatically in Fig. 6, Plate I.

The vessels of the first group run cephalad, two on the dorsal side and two on the ventral side of the alimentary canal. They are embedded in the adipose tissue and follow the digestive tract in a more or less irregular or wavy path throughout most of its length. They extend forward as far as the crop and here turn caudad and follow the mid-intestine rather closely to its posterior end. At this point they leave the mid-intestine and follow an irregular course through the

fatty tissue and the body cavity in the region of the pyloric valve. Finally two tubules from the first group unite at their distal ends, forming a common stem on the dorsal side near the anterior part of the colon. Immediately posterior to the union of these two tubules one of the tubules of the second group joins this same stem, forming a common duct. This formation of a common duct is quite similar to that described for Halitica bimarginata Say (Woods, 1916). The three remaining tubules form a similar grouping on the ventral side of the colon.

The two tubules which make up the second group are smaller in size and shorter in length than those of the first. They follow an irregular course in the body cavity, being closely associated with the ileum and colon, finally each uniting with one of the common stems as described in the preceding paragraph.

These two common stems, one dorsal and the other ventral, enter the peritoneal membrane of the colon and immediately separate into the six original Malpighian tubules. They follow a straight path a short distance and gradually increase in size, becoming flattened and convoluted in shape as they approach the posterior end of the colon. They do not branch but simply follow a very irregular course (Fig. 6, Plate I), bending and folding back on themselves until the posterior part of the colon is almost completely covered with a mass of convoluted Malpighian tubules. The tubules terminate blindly at the junction of the colon and rectum.

The ileum, frequently called the small intestine, is a small tube which connects the stomach with the colon. It extends posteriorly to about the ninth abdominal segment, and then turns sharply cephalad joining the colon in the seventh abdominal segment.

The colon connects the ileum with the rectum. At its anterior end it is almost the same size as the ileum but gradually increases in size posteriorly, reaching its maximum diameter just before the junction with the rectum.

The rectum is short and heavily muscled, and is of the same diameter as the oesophagus, as shown by sections of this area. It connects the colon with the anus.

Histology of the Alimentary Canal.

Fore-Intestine.

The histological examination of the fore-intestine did not reveal any unusual structures. It is lined throughout with a rather heavy layer of chitin or intima. This layer is non-cellular and almost transparent, and is very difficult to stain. It projects into the lumen of the pharynx and oesophagus in irregular wave-like folds. As the oesophagus (Fig. 1, Plate I) gradually enlarges to form the crop (Fig. 2, Plate I), these folds become less pronounced.

The epithelium forms a single layer of rather flattened, irregular shaped cells with prominent nuclei. This layer of cells lies next to the intima and follows the wave-like folds throughout the fore-intestine. The cell walls are not very distinct, but the basement membrane is quite evident.

Outside of the epithelial layer are found well developed bundles of longitudinal muscle fibers. These are quite evident in all the sections of the fore-intestine but they gradually become smaller in the region of the crop.

Surrounding the longitudinal muscles is a well developed layer of circular muscle. These muscles are numerous in the folds of the oesophageal valve.

The oesophageal valve, (Fig. 4, Plate I), marks the junction of the fore-intestine with the mid-intestine. It consists of six folds which project into the lumen of the stomach. These folds are formed by the projection of the fore-intestine into the mid-intestine, which then fold back upon themselves in an outward direction to the anterior edge of the mid-intestine. At this point the intima of the fore-intestine ends and the digestive epithelium of the stomach begins. The epithelium of the valve is continuous with that of the fore-intestine. Circular muscles are numerous in the folds of the valve and they apparently function in its closing. The circular and longitudinal muscles reverse their positions at the point where the intima ends and the digestive epithelium begins. Strands of peritoneal membrane are evident in sections from this region.

Mid-Intestine.

The mid-intestine or stomach is that part of the alimentary canal posterior to the oesophageal valve and anterior to the pyloric valve.

In this part of the digestive tract there is no cuticular covering of the epithelial cells, and the position of the circular and longitudinal muscle layers is reversed as compared with that in the fore-intestine.

The peritrophic membrane, which is a structureless membrane found in the mid-gut, encloses the food in the stomach thus protecting the delicate secreting cells from injury by sharp food particles. It is apparently secreted near the juncture of the fore-intestine and the mid-intestine, since the sections showing it were from the anterior part of the mid-gut (Fig. 11, Plate II).

The cells of the digestive epithelium vary in size and shape depending upon their physiological condition at the time the insect was killed. In the specimens dissected which had fed very recently or were feeding prior to the time of killing, the epithelial cells are of the columnar type, being long and narrow (Fig. 11, Plate II), and showing holocrine secretion; while the epithelial cells in the specimens which were killed a few hours after feeding are much shorter, indicating that the epithelium had recently secreted. In general the epithelial cells are shorter in the posterior part of the mid-gut, (Fig. 5, Plate I). The nuclei are large and oval in shape, staining deep blue with Delafield's Haemotoxylin.

The secretion of the epithelial cells is holocrine, the entire contents of the cell bursting out into the lumen of the gut, after which the cell is replaced by new cells developed from nidi (nests of embryonic tissue scattered in the base of the epithelium). The nidi (Fig. 11, Plate II) are numerous and lie in the base of the epithelium along the basement membrane. The columnar cells burst as the digestive fluids are needed,

and they are replaced by new cells splitting off on the sides of the nidi, which lengthen and fill with digestive fluid.

The circular muscles of the stomach consist of two narrow layers which are fairly well developed, and are present throughout the length of the mid-gut.

The outer layer of the stomach consists of small strands of longitudinal muscle.

The thin delicate peritoneal membrane is also present.

Hind-Intestine.

The hind-intestine is marked anteriorly by the pyloric valve and posteriorly by the anus.

The pyloric valve (Fig. 5, Plate I) consists of very narrow columnar cells which are arranged in irregular fan-shaped groups. The intima which lines the valve and continues throughout the hind-intestine originates at the junction of the mid- and hind-intestine. These fan-shaped groups of cells probably function as a valve, since this region is surrounded by a heavy layer of circular muscle which upon contraction apparently could close the valve.

The Malpighian tubule attachments have been described under gross anatomy of the alimentary canal. Histological examination of the tubules at their respective points of origin shows that the epithelial cells are very similar to those cells making up the pyloric valve, being narrow and elongate and having conspicuous nuclei. Later they assume the characteristic cuboidal shape a short distance from the point of attachment. Intima is present in the tubules but is difficult to detect a short distance from the point where they join the ileum. In a typical cross-section they are made up of from four to six cuboidal cells with large conspicuous nuclei, and are surrounded by a very thin peritoneal membrane (Fig. 3, Plate I). A cross section from A to B in Fig. 5, Plate I, is shown in Fig. 7, Plate II. This shows the opening through which the excretions from the Malpighian tubules of the first group must pass in entering the ileum.

There is a gradual change from the region of the valve to that of the ileum, the intima becoming more wavy in outline, the epithelial cells and their nuclei becoming larger in size, and the circular muscles decreasing slightly in size. The longitudinal muscles consist of a few isolated strands.

The ileum (Fig. 8, Plate II) forms the connecting link between the pyloric valve and the colon. The layers of intima, epithelium, basement membrane, and circular and longitudinal muscle of the ileum are continuous with those of the colon. In the colon the folds of the intima are less pronounced, and the epithelial cells are slightly larger.

The circular muscles consist of a single layer which is prominent at the anterior part of the colon but gradually decreases in size towards the posterior end.

The longitudinal muscles are fairly well developed at the anterior end and gradually increase in size posteriorly.

The distal ends of the Malpighian tubules also form a layer around the colon. The entrance of the tubules into the delicate nucleated

layer of peritoneal membrane was described under gross anatomy. A cross section of the anterior part of the colon shows the six Malpighian tubules (Fig. 9, Plate II) in the peritoneal membrane.

Proceeding caudad serial sections of the colon show an increasing number of sections of Malpighian tubules. This is due to the convoluted shape of the tubules and the winding course followed by them in the posterior part of the colon. A cross section of the extreme posterior part (Fig. 10, Plate II) shows almost a continuous layer of Malpighian tubules around the colon, which would seem to indicate that the tubules branch.

Woods (1916) states that the Malpighian vessels of *Haltica bimarginata* Say seem to branch irregularly. It was found that they do not branch but follow a very irregular course (Fig. 6, Plate I) in the peritoneal layer. The colon is almost completely covered with tubules near the posterior end, so that in a cross section of this region a number of sections of the same tubule are made, thus forming a continuous layer. The tubules end blindly in the peritoneum at the junction of the colon and rectum.

The rectum connects the colon with the anus. The colon ends rather abruptly and the heavy circular muscle layers mark the beginning of the rectum. The intima and epithelium project into the lumen of the rectum in from five to eight wavy folds, (Fig. 12, Plate II), these becoming more pronounced posteriorly. The nuclei of the epithelial cells are large, the cell walls being indistinct and the cells being somewhat smaller than those of the colon. Outside of the epithelial cells is the basement membrane, which is fairly distinct. The circular muscles are well developed and are composed of three or four layers. Longitudinal muscle is present in a few isolated strands.

SUMMARY.

Morphologically the canal is divided into three primary regions, namely, fore-intestine, mid-intestine, and hind-intestine.

The fore-intestine is represented by the following parts; pharynx, oesophagus, crop, and oesophageal valve.

The mid-intestine is represented by the stomach.

The hind-intestine consists of the following regions; pyloric valve, Malpighian tubules, ileum, colon, and rectum.

Histological examination of the fore-intestine reveals a similarity in structure of the various parts. The layers represented from within out are: intima, epithelium, basement membrane, longitudinal muscle, circular muscle, and peritoneal membrane.

In the mid-intestine the layers from within out are: peritrophic membrane, epithelium, basement membrane, circular muscle, longitudinal muscle, and peritoneal membrane.

The layers in the hind-intestine from within out are: intima, epithelium, basement membrane, circular muscle, longitudinal muscle, and peritoneal membrane.

There are six Malpighian tubules present in *Criocerus asparagi* Linn. The distribution of these tubules is as follows, beginning at their distal ends. From their point of attachment at the distal end of the colon, the tubules follow a convoluted course running cephalad in the peritoneal membrane. They unite at the anterior end of this region to form two common trunks. These two trunks upon leaving the wall of the colon, each split into a single tube and a common stem representing a pair of tubes. The single tubes follow an irregular course in the region of the ileum and finally become attached to an evagination of the epithelium of the pyloric valve. Each common stem soon separates into two tubules which have a long course in the body cavity, running cephalad to the crop. Here they turn caudad following the mid-gut to its posterior end, where the four vessels unite to form a knob-like structure or urinary bladder, which empties into the hind-intestine just posterior to the pyloric valve.

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EXPLANATION OF PLATES.

PLATE I.

Fig. 1. Cross-section of oesophagus.
Fig. 2. Cross-section of crop.
Fig. 3. Cross-section of Malpighian tubule.
Fig. 4. Longitudinal section of oesophageal valve.
Fig. 5. Longitudinal section of pyloric valve. This section also shows the posterior part of the stomach, the anterior part of the ileum, and the duct formed by the attachment of the group of four Malpighian tubules.
Fig. 6. Diagrammatic dorsal view showing alimentary canal and Malpighian tubules. The Malpighian tubules on the colon are in the peritoneal membrane.

PLATE II.

Fig. 7. Cross-section from A to B in Fig. 5, Plate I, showing the duct of the group of four Malpighian tubules.
Fig. 8. Cross-section of ileum.
Fig. 9. Cross-section of anterior part of colon, showing the six Malpighian tubules in the peritoneal membrane.
Fig. 10. Cross-section of the posterior part of the colon showing a continuous layer of tubules in the peritoneal membrane.
Fig. 11. Cross-section of stomach showing the peritrophic membrane and holocrine secretion.
Fig. 12. Cross-section of rectum.

KEY TO ABBREVIATIONS.

B. M.—Basement membrane.
C. D.—Common duct.
C. M.—Circular muscle.
CR.—Crop.
CO.—Colon.
DU.—Duct.
EPI.—Epithelium.
IL.—Ileum.
INT.—Intima.
L. M.—Longitudinal muscle.
M. I.—Mid-intestine.
M. T.—Malpighian tubule.
M. T. A.—Malpighian tubule attachment.
NI.—Nidus.
OES.—Oesophagus.
OES. V.—Oesophageal valve.
PH.—Pharynx.
PER. M.—Peritrophic membrane.
P. M.—Peritoneal membrane.
P. V.—Pyloric valve.
REC.—Rectum.

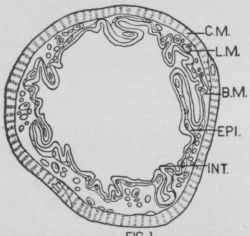


FIG. 1.


FIG. 3.

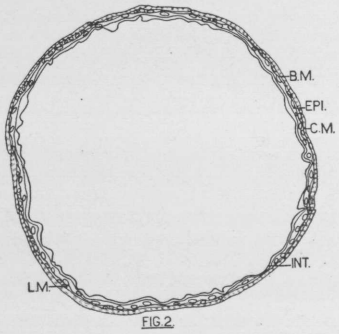
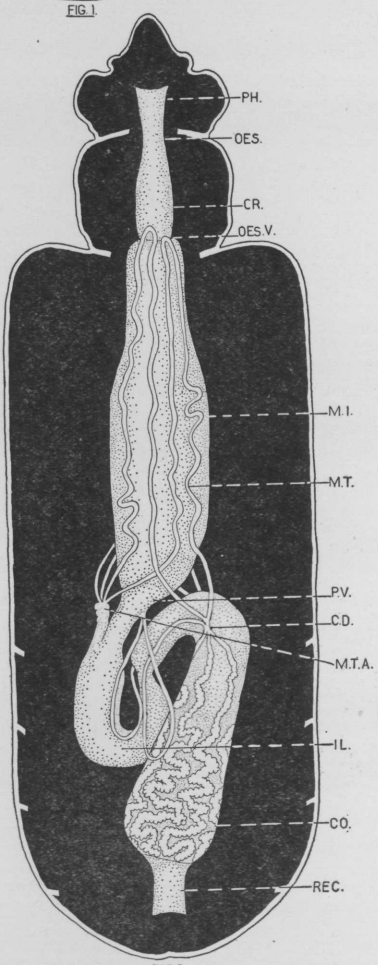


FIG. 2.



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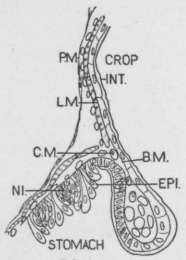

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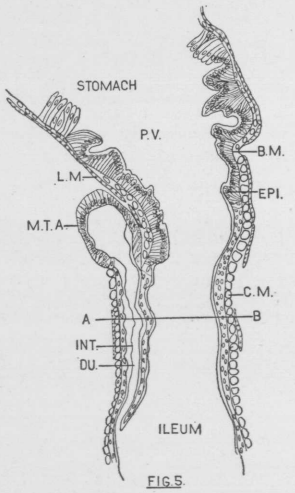

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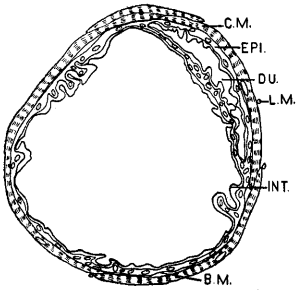


FIG. 7

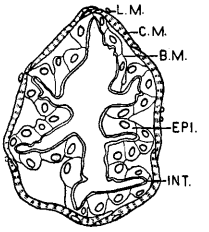


FIG. 8.

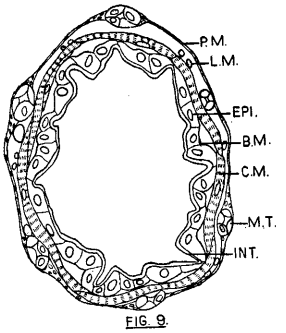


FIG. 9.

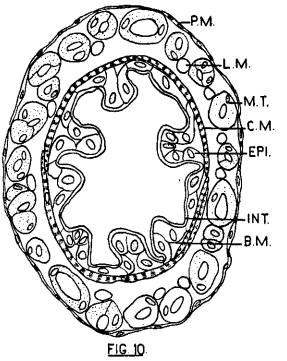
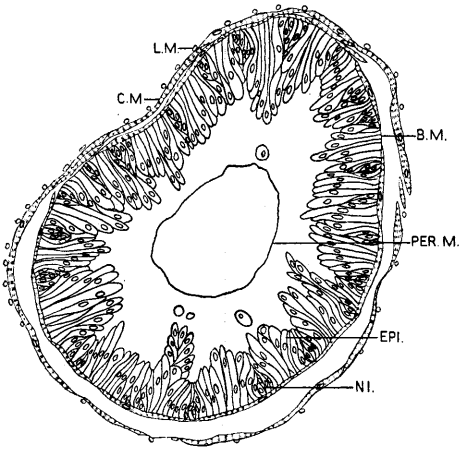


FIG. 10



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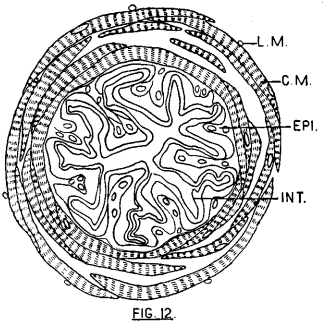

FIG. 12.